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Interspecific differences in population trends of Spanish birds are related to habitat and climatic preferences

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ABSTRACT

Aim Animal monitoring programmes have allowed analyses of population trends, most of which now comment on the possible effect of global climate change. However, the relationship between the interspecific variation in population trends and species traits, such as habitat preferences, niche breadth or distribution patterns, has received little attention, in spite of its usefulness in the construction of ecological generalizations. The objectives of this study were: (1) to determine whether there are characteristics shared among species with upwards or downwards trends, and (2) to assess whether population changes agree with what could be expected under global warming (a decrease in species typical of cooler environments).

Location The Spanish part of the Iberian Peninsula (c. 500,000 km²) in the south-western part of the Mediterranean Basin.

Methods We modelled recent breeding population changes (1996–2004), in areas without apparent land use changes, for 57 common passerine birds with species-specific ecological and distributional patterns as explanatory variables.

Results One-half of these species have shown a generalized pattern towards the increase of their populations, while only one-tenth showed a significant decrease. One half (54%) of the interspecific variability in yearly population trends is explained considering species-specific traits. Species showing more marked increases preferred wooded habitats, were habitat generalists and occupied warmer and wetter areas, while moderate decreases were found for open country habitats in drier areas.

Main conclusions The coherent pattern in population trends we found disagrees with the proposed detrimental effect of global warming on bird populations of western Europe, which is expected to be more intense in bird species inhabiting cooler areas and habitats. Such a pattern suggests that factors other than the increase in temperature may be brought to discussions on global change as relevant components to explain recent changes in biodiversity.

Keywords

Global change, habitat breadth, habitat preferences, Iberian Peninsula, population trends, Spain.

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INTRODUCTION

The analysis of animal population trends has long attracted the attention of researchers dealing with natural systems to address theoretical (Davidson & Andrewartha, 1948; Clutton-Brock *et al.*, 1983; Pribil & Houlahan, 2003) and applied conservation problems (Fewster *et al.*, 2000). As a result of the growing concern with the loss of biodiversity (Pimm & Raven, 2000; Thomas

et al., 2004a), the survey of animal populations has acquired great relevance, with monitoring being urged in strategic programmes and a plethora of projects being developed by governmental agencies and conservationist organizations (CEC, 2001; Sauer *et al.*, 2003; Vorisek & Marchant, 2003). Furthermore, both long- and short-term changes in population numbers are being used to define the international conservation status of species (e.g. 3–10 years in IUCN, 2001).

The study of population trends for a wide range of species further allows for the exploration of common interspecific patterns, to infer general mechanisms underlying variations in population levels as a consequence of environmental changes (Lawton, 1996; Gaston, 2000; Gaston & Blackburn, 2000). Global climatic change has been proposed as one of the most likely environmental processes governing population trends (McCarty, 2001; Stenseth *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003) and is thus receiving a lot of attention from researchers (Thomas & Lennon, 1999; Moss *et al.*, 2001; Peterson *et al.*, 2002; for papers dealing with birds see Butler, 2003; Sanz, 2003; Thomas *et al.*, 2004b). However, among the studies focused on population trends, only a few have aimed to relate them to species traits such as ecological niche, distribution patterns or negative impacts suffered from human activities (McKenzie *et al.*, 2003; Pribil & Houlahan, 2003; for hunting and landscape transformation see Julliard *et al.*, 2004a; Meynecke, 2004). For example, it has been hypothesized that species preferring low environmental temperatures, which inhabit cooler habitats or areas, would be negatively affected by global warming as a consequence of the widely accepted increase of temperature during the last two decades (Grabherr *et al.*, 1994; Julliard *et al.*, 2004a). This effect is assumed to be more intense at higher latitudes and altitudes because these areas seem to be changing more rapidly (Myneni *et al.*, 1997; Briffa *et al.*, 1998). Also new global effects other than change in temperature that might influence bird population cycles have recently been reported (Stanhill & Cohen, 2001). Nevertheless, a wide variety of results have been obtained working with different species and regions, showing that the patterns are species-specific and area dependent (Gill *et al.*, 2001; Visser *et al.*, 2003; Archaux, 2004; Julliard *et al.*, 2004a; Gregory *et al.*, 2005). Hence the need to gather repeatable and consistent patterns in very different taxonomic and geographical contexts to build ecological generalizations and models, an approach similar to that pursued in the macroecology programme (Gaston & Blackburn, 2000).

In this paper we analyse the association between recent population changes in the common birds of the Iberian Peninsula and species-specific characteristics related to habitat preferences, population density, habitat breadth and climatic characteristics of their geographical ranges. We study bird trends in a time window of 9 years that represents the longer time series for a national biodiversity survey in Spain. This is the first analysis on the change of bird populations in the Mediterranean region. We hypothesize that species that preferentially occupy cooler habitats and wetter areas (which in the Iberian Peninsula equates to forests in mountain or northern territories) do worse in a scenario of climate warming. Also, migratory birds could show more decreasing trends given the higher potential for a global change-induced mismatch between the different resources they need during the wintering and breeding periods (Sanz, 2002; Böhning-Gaese & Lemoine, 2004; Julliard *et al.*, 2004a). Finally, habitat breadth is included as a potential explanatory variable since it has been previously shown to have a positive correlation with population trends (Siriwardena *et al.*, 1998; Julliard *et al.*, 2004a).

Our main goals are: (1) to test if bird populations in Spain are decreasing, considering the generalized idea about decreases in bird populations of western Europe in the last two decades (Crick, 2004; Julliard *et al.*, 2004a); (2) to test if the observed changes in bird populations in Spain are consistent with predictions related to climate change – that is, we might expect a negative effect of global warming on bird species inhabiting cooler areas and habitats, and a positive influence on species of xeric areas and environments (see references above); and (3) to infer shared species-specific characteristics determining the proneness to consistent yearly changes towards the increase or decrease of populations.

METHODS

Study area and species data

The Spanish SACRE programme (monitoring of common breeding birds in Spain) began in 1996 and is devoted to surveying a random selection of Spanish 10 × 10 km Universal Transverse Mercator (UTM) squares for monitoring population changes of common bird species during the breeding season (SEO/BirdLife, 2004). Our study period (1996–2004) relates to a time window equivalent to other time spans used to define short-term trends in monitoring programmes (IUCN, 2001; Eaton *et al.*, 2004). In each UTM square, a minimum of 20 5-min morning point count stations are arranged to cover all habitats in proportion to their surfaces. Stations are visited twice (once in April–May and again in May–June) to allow for detection of early breeders and late migrants. The SACRE survey assigned squares to volunteers according to a random scheme, but those further from main cities were more difficult to assign and more likely to end up being dropped out. In this study we have considered 394 UTM squares sampled on the Iberian Peninsula, covering most of the latitudinal and longitudinal span in the Iberian Peninsula (the selected squares were sampled for at least 6 years, Fig. 1). We have not included in our sample those UTM squares that have undergone changes in the extent of the sampled habitats throughout the study period of 9 years. Therefore, the observed population trends have not been affected by fragmentation or conversion of native habitats, nor by reforestation efforts. The Iberian Peninsula is located at the south-western edge of the Western Palearctic, between 36° N and 43° N. The study area shows major gradients in climate (temperature, rainfall) that are regionally modified by numerous mountain ranges (up to 3481 m above sea level) and the distance to the sea. More locally, habitat diversity is increased by a considerable variation in soil age and mineral characteristics. Human activity was prevalent during the Holocene, thus adding more heterogeneity to this ecological scenario. Consequently, habitats are diverse and the rich bird fauna comprises a large number of species with different ecological niches (Blondel & Aronson, 1999). We selected fairly common and widespread species, considering those which have been recorded in more than 75 UTM squares in at least 5 years (the sample size for all species was finally larger than 35 UTM squares in any year).



Figure 1 Study areas in the Spanish sector of the Iberian Peninsula. Shown in black are the 10×10 km UTM squares selected for the analyses.

Population trends were calculated using Poisson (log-linear) regression with the program TRIM (Pannekoek & van Strien, 2003), which is designed to analyse time series of counts with missing observations (see Gregory *et al.*, 2005, for another example of the use of this technique). Missing counts for the sampling units (the 10×10 km UTM square) are imputed from the values on the rest of the sample, and serial correlation and overdispersion are taken into account by estimating log-linear models with generalized estimating equations. Population trends were then taken as the linear trend of the model-based total counts for each year (the 'overall trend with intercept' settings in TRIM). These raw analyses were provided by the Sociedad Española de Ornitología (SEO/BirdLife).

The studied species were Passeriformes, for which extensive surveys based on point counts are considered worldwide to be particularly suitable for monitoring population trends (Bibby *et al.*, 2000; Julliard & Jiguet, 2002). The selected 57 species of Passeriformes show a wide range of distribution and ecological patterns summarized in previously published work (Hagemajjer & Blair, 1997; Carrascal & Lobo, 2003; Martí & Del Moral, 2003). These facts allow us to analyse interspecific differences in yearly population changes according to autecological traits. For each one of the 57 Passeriformes, we obtained the following variables: (1) migratory strategy (1, trans-Saharan migrants; 0, resident species not migrating outside the Iberian Peninsula); (2) the distribution area of each species (number of occupied 10×10 UTM km squares) from the national breeding bird atlas (Martí & Del Moral, 2003); (3) maximum ecological density in the Iberian Peninsula (the average of the three highest densities, obtained by the line transect method with survey belts of 25 m at each side of the transect, recorded in the most favourable habitats for each species; from Carrascal & Lobo, 2003); (4) an index of the average structural complexity and vegetation volume (SC) of preferred habitats of the bird species (see below and Polo &

Carrascal, 1999, for a similar approach) obtained from Carrascal & Lobo (2003); (5) habitat breadth (HB) of the bird species in six habitat categories (obtained from Carrascal & Lobo, 2003; see below). HB was calculated using Levin's index (Levins, 1968); (6) average June temperature and spring precipitation in the occupied 10×10 km UTM squares.

Maximum ecological densities in the Iberian Peninsula obtained from Carrascal & Lobo (2003) are not absolute densities because the detectability of bird species is not 100% within the census belts of 25 m. Therefore, the maximum density estimations should be interpreted as relative abundances. Nevertheless, these relative abundances are very similar to absolute densities, as the detectability of many bird species within the narrow belts of 25 m is very high (between 0.75 and 0.98 depending on the species; L.M. Carrascal and J. Seoane, unpublished data). Thus, this issue is not a big problem in our analysis because the interspecific variation of detectability within the belts of 25 m at each side of the observer is many times lower than the natural interspecific variation in relative abundance (between 0.74 and 60.3 birds/10 ha; see Appendix). We included the species distribution area and abundances as potential explanatory variables of population trends to control for the possible effect of relative rarity (populations with scarce individuals or occupied localities may be more vulnerable to environmental changes and may thus exhibit decreasing trends).

The index of structural complexity and vegetation volume (SC) ranged from 0 to 5 and was obtained for a compilation of 305 census localities by Carrascal & Lobo (2003) using six habitat categories: 0, lacking or very sparse vegetation cover; 1, pasturelands; 2, shrublands with sparse vegetation cover made up of bushes lower than 0.5 m; 3, thick shrublands with bushes higher than 0.3 m in height; 4, parklands, narrow riparian woods, hedgerows and young forests; 5, dense mature forests with trees usually higher than 12 m. These scores are highly correlated with

vegetation volume and structural complexity of habitats, providing a simple way to synthesize, at a coarse-grained scale, the habitat structure of published information on bird abundance in different localities and environments. The weighted mean of SC for each species was calculated taking into account the relative abundances (birds/10 ha) of species in the compilation of census localities and their structural complexity index. These weighted means are used to describe the average complexity of habitats preferred by each species. The index was used to test whether population trends were independent of general habitat preferences of bird species according to vegetation volume and habitat structural complexity.

We also calculated the average 'position' of the 57 species in the plane formed by two climatic variables related to spring precipitation (April–June; i.e. the breeding season for the studied avifauna), and June temperature (i.e. temperature at the end of the breeding season when fledgling emancipation begins). These values represent the average climatic characteristics of the distribution ranges of the species in the Iberian Peninsula, ordering them along dry–wet and warm–cool gradients. The climatic data were extracted from the CLIMATE data base version 2 (<http://portal.pik-potsdam.de/members/cramer/climate.html>) and can be looked up or obtained from the *Atlas virtual de las aves terrestres de España* (<http://www.vertebradosibericos.org/aves/atlas/blqpdf/blq50.html>). The average 'position' of each species was obtained by averaging the two climatic variables in the occupied 10×10 UTM squares in Spain.

Statistical analyses

Interspecific differences in short-term population trends among Passeriformes were related to species-specific ecological traits by means of multiple regression analysis using the species as the sample unit ($n = 57$). The response variable was the instantaneous growth rate (i.e. the additive slope of the linear trend of population counts with time), which was normally distributed (Shapiro–Wilk test of normality: $P = 0.395$). The predictor variables were migratory strategy (included as a dummy variable), maximum relative abundance, average structural complexity of preferred habitats, distribution area, habitat breadth and the average June temperature and spring precipitation of the occupied 10×10 km UTM cells (see the paragraph above). We tested for deviations from linearity of continuous predictor variables on instantaneous growth rate by means of including their quadratic terms in the regression model, and by exploring the scatter plots of residuals of the regression model against the predictor continuous variables. There was no indication that the relationships with species trends were nonlinear. As the precision of the growth rate depends on the sample size (i.e. number of occupied UTM squares fed into the trend analysis) and the residual temporal variation of abundance around the linear trend (i.e. variation of annual population estimations around the linear long-term tendency), we used the multiple regression analysis weighing the estimates of each species by the inverse of the squared standard error (SE) of the instantaneous growth rate (see also Julliard *et al.*, 2004a). This approach gives more weight to those species

with larger sample sizes and those whose models explain more deviance of the short-term population trends.

Bird species are evolutionarily related throughout a phylogenetic scheme, and therefore they should not be treated as independent sample units (Harvey & Purvis, 1991). This has been established as a common paradigm in evolutionary ecology research, although it is subjected to controversy and debate (Westoby *et al.*, 1995; Price, 1997). Several authors have pointed out that on many occasions similar results are obtained in phylogenetic and non-phylogenetic analyses (e.g. Price, 1997; Shultz *et al.*, 2005), and that in some instances ecologists are not interested in patterns of biological diversification across evolutionary time but only in present-day relationships comprising non-evolutionary associations under human-transformed environments. Because we study the relationships among ecological traits of species and their present-day distribution derived from censuses in a transformed landscape, we have simplified the data analyses, thereby avoiding the complexities and drawbacks of comparative methods (i.e. uncertainty about models of evolutionary change, phylogeny topology or branch lengths).

RESULTS

There was a considerable interspecific variation in bird population changes across time between 1996 and 2004 (range of slopes: $-0.032/0.094$). Average instantaneous growth rate for the 57 studied passerine species was significantly higher than zero (i.e. the null hypothesis of random population trends; mean = 0.022, SD = 0.030; $t = 5.505$, $P < 0.001$). Twenty-nine species significantly increased their populations, while six species showed significant decreasing trends: skylark (*Alauda arvensis*), crested lark (*Galerida cristata*), calandra lark (*Melanocorypha calandra*), swallow (*Hirundo rustica*), woodchat shrike (*Lanius senator*) and jackdaw (*Corvus monedula*; see Appendix). During this recent time period, the mean temperature of the breeding season in Spain has been increasing, which agrees with the global long-term trend towards higher temperatures (IPCC, 2001; Moreno, 2005; see Fig. 2).

The average instantaneous growth rate did not differ significantly ($t = 1.603$, 13 d.f., $P = 0.089$) between the species from cool environments widely spread in northern and central Europe, and whose southern limits currently occur in the Iberian Peninsula (*Aegithalos caudatus*, *Alauda arvensis*, *Corvus corone*, *Parus cristatus*, *Passer montanus*, *Phylloscopus collybita*, *Sylvia communis* and *Turdus philomelos*; mean = 0.0303, SD = 0.034, $n = 8$), and those species from dry and warm environments mainly distributed in the south-western limit of the Western Palearctic and extending further south into North Africa (*Calandrella brachydactyla*, *Melanocorypha calandra*, *Oenanthe hispanica*, *Sturnus unicolor*, *Sylvia cantillans*, *Sylvia melanocephala* and *Sylvia undata*; mean = 0.0005, SD = 0.028, $n = 7$).

A detailed analysis of the interspecific variation in yearly changes in bird numbers, related to autecological parameters of Passeriformes, is shown in Table 1. Simple correlations (r) show that population trends were significantly and positively correlated

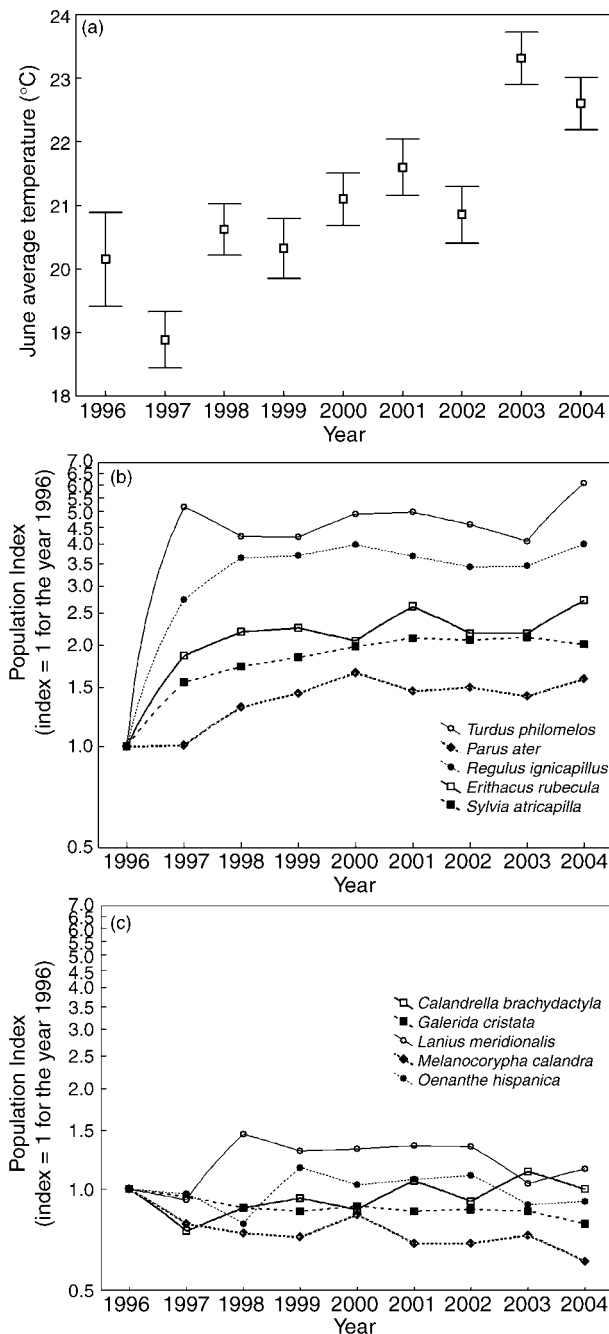


Figure 2 Variation of average temperature and population index of several passerine species in the Spanish sector of the Iberian Peninsula from 1996 to 2004. (a) Variation [mean \pm 1 standard error (SE)] of June temperature in a representative sample of 46 localities. (b) Population index variation for five passerine species mainly distributed in cool and wet areas and representative of woody environments. (c) Population index variation for five passerines representative of open-country habitats and mainly distributed in dry and hot sectors. Population indices are the abundances predicted by the Poisson regression of trends on bird counts, standardized to having 1 as the value for the first study year (1996). Temperatures in June have been taken as a summary of the breeding period for bird species throughout the study area. Data obtained from the Spanish Instituto Nacional de Estadística (<http://www.ine.es/inebase/indexi.html>). Data for species taken from SEO/BirdLife (2004).

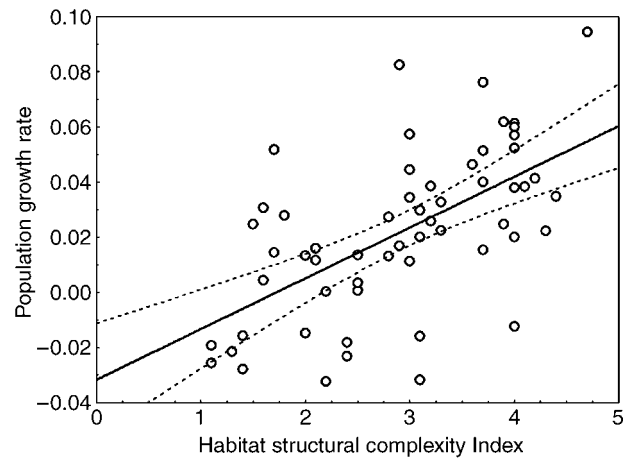


Figure 3 Relationship between population yearly changes in bird counts of 57 passerine species in Spain (instantaneous growth rate measured as the additive regression slope of population counts in 20 sites per UTM square with time) and the average structural complexity of their preferred habitats [ranging from 0 (lacking or very sparse vegetation cover) to 5 (dense mature forests with trees higher than 12 m)]. For statistical details see Table 1.

with the structural complexity index of preferred habitats, habitat breadth and spring rainfall.

The multiple regression model accounted for 54.2% of the observed interspecific variability in population trends ($F_{7,49} = 8.28, P < 0.00001$). Population trends from 1996 to 2004 were significantly and positively related to structural complexity index of preferred habitats (Fig. 3), and distribution preferences for warmer and wetter sectors within the Iberian Peninsula [see partial effects controlling for the other predictor variables (beta), and variance accounted for each effect in Table 1]. Non-significant partial effects were found for migratory status, maximum relative abundance, habitat breadth and the extent of the geographical range in Spain (less than 1% of the original variance explained). An important amount of the explained variance was accounted for by the combined effects of the predictor variables (23%).

DISCUSSION

European bird population trends are not geographically generalizable, or may differ according to coarse habitat preference patterns (Gregory *et al.*, 2005). We found that one-half of the study species show significant increasing recent trends despite the public concern that bird populations are generally decreasing (Krebs *et al.*, 1999; Julliard *et al.*, 2004a; Raven *et al.*, 2004). Similarly, one-half of terrestrial passerine birds in the United Kingdom exhibited increasing recent trends in a very similar time period (1994–2004), showing that the stated concern for decreasing trends in common species is not generalizable across taxa (Raven *et al.*, 2005, see <http://www.bto.org/birdtrends2006/>). There is also a marked consistency between the observed increasing trends for forest and open woodland species in the Iberian Peninsula and at more northern European latitudes in the same recent years (Gregory *et al.*, 2005).

Table 1 Results of weighted multiple regression carried out with 57 passerine species in Spain, to analyse interspecific variation in yearly change in bird numbers (additive slope measuring instantaneous growth rate) related to species' autecological and distributional patterns (type III variance decomposition). Weights were the inverse of the squared standard error of population trends of each species.

	<i>r</i>	Multiple regression		
		beta	% var.	<i>P</i>
Migratory status (1, trans-Saharan migrant; 0, resident)	-0.03	0.11	1.05	0.287
Maximum ecological abundance (Dmax; log)	0.09	0.04	0.11	0.755
Structural complexity index (SC)	0.69***	0.58	21.17	< 0.001
Habitat breadth (HB)	0.30*	0.12	1.04	0.287
No. UTM 10 × 10 km occupied in Spain (no. UTM)	0.09	0.03	0.07	0.814
Average temperature (June)	-0.09	0.36	3.93	0.041
Spring precipitation (April–June)	0.35**	0.39	3.95	0.035

r, simple correlation between yearly change in bird numbers and each predictor variable (*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$); beta, standardized partial regression coefficient; % var., percentage of variance accounted for each effect (an additional 23.11% of the explained variance is attributable to the combined effect of the seven predictor variables).

Our results clearly show that interspecific variation in the yearly population trends between 1996 and 2004 can be explained considering species-specific ecological traits. During the study period, the species whose populations have increased more markedly in the Iberian Peninsula were mainly those with preferences for wooded habitats that occupy warm areas with high precipitation during the breeding season. The remaining species with converse ecological and biogeographical traits experienced slight decreases or did not show any consistent pattern of change in bird population between 1996 and 2004.

Temporal changes in bird counts could partly be attributed to an improvement in observers' identification skills throughout the study period, particularly in large-scale monitoring programmes where the sampling is carried out by amateurs (Kendall *et al.*, 1996). However, this is unlikely to greatly affect our study because the SACRE monitoring programme is a young initiative that still has a limited number of participants, most of whom were already skilful birders when they joined the programme. Moreover, we strictly selected the UTM squares to analyse, disregarding those only recently surveyed and thus making less probable any bias due to observer learning. However, we tested this possibility by comparing the estimates of yearly population change between conspicuous, easily recognized species ($n = 18$, see Appendix) and the rest of the species ($n = 39$), and we failed to detect any differences ($t = 0.680$, $P = 0.499$).

Julliard *et al.* (2004a), working with 77 common bird species in France, found that species with large ecological breadth showed a tendency to increase their numbers throughout the analysed period. That is, habitat specialization is related to declining rates: generalist species are declining at a much lower rate than specialists. Rarity, in terms of small extent of occupancy, low population size and abundance, has been shown to be associated with greater probabilities of extinction because rare species are more sensitive to catastrophic events or to small population problems, such as the Allee effect (Shaffer, 1981; Stephens & Sutherland, 1999). Habitat breadth was marginally related to

population trends in Spain (significant simple correlation, but non-significant partial relationship when removing the effect of other predictors): habitat generalist species were declining at a much lower rate than habitat specialists (see also Siriwardena *et al.*, 1998). On the other hand, neither the number of occupied UTM squares nor the maximum ecological densities were associated with population trends in our study. However, it should be noted that we base our analyses on a set of common species (the rarer of which occupies 1456 10 × 10 km UTM squares), and thus we are not able to detect the effects of extreme rarity and habitat specialization, given that only relatively widespread Passeriformes were included in the analysis (but see Caughley & Gunn, 1996, for several examples of long-term population stability of rare species). Similar to the findings of Siriwardena *et al.* (1998) and Julliard *et al.* (2004a), we did not detect a significant effect of migratory status on yearly population trends, although migratory birds have been suggested to be at particularly high risk (for example, due to phenological miscuing, Crick, 2004).

The Earth's climate has been warming over the last century, and particularly in the last three decades (Karl & Trenberth, 2003; Solanki & Krivova, 2003). Studies on the effects of climate change on animal and plant populations normally describe a detrimental effect of year, as a surrogate of temperature rise, on some biological parameters (e.g. population numbers, breeding phenology: Crick & Sparks, 1999; Parmesan *et al.*, 1999; Moss *et al.*, 2001; and see Sanz, 2002, for a review in the Mediterranean region). Considering these associations, global warming has been proposed as the main cause of biodiversity deterioration and population reductions (Stenseth *et al.*, 2002; Walther *et al.*, 2002; Thomas *et al.*, 2004a), especially in those species preferring low environmental temperatures that inhabit cooler habitats or areas at higher latitudes and altitudes (Myneni *et al.*, 1997; Briffa *et al.*, 1998; Julliard *et al.*, 2004a). Our results, however, do not support these tendencies, although the mean temperature of the breeding season in Spain has been increasing from 1996 to 2004, which agrees with the global long-term trend towards higher

temperatures (IPCC, 2001; Moreno, 2005; see Fig. 2). It could be argued that the effects of global warming on population trends would mainly be noticeable in species whose limits actually occur in the area of study, because it is at the range margins where climate change is most likely to affect population numbers (see also Julliard *et al.*, 2004b). However, the average instantaneous growth rate did not differ significantly between the species mainly distributed in the south-western limit of the Western Palearctic and extending further south into North Africa, and those species widely spread in northern and central Europe, and whose southern limits actually occur in the Iberian Peninsula. Indeed, the slopes of the instantaneous growth rates for both groups show a difference contrary to that expected considering the effects of global warming on short-term population trends (i.e. more negative trends in species from cool environments widely spread in northern European latitudes).

These results suggest the need for considering other alternatives to temperature as an explanatory phenomenon for the observed patterns of population increases. The results of several studies indicate that there has been an increase in plant growth or terrestrial net primary production in middle latitudes of the Northern Hemisphere since the 1980s, particularly in forest environments, probably due to changes in the amplitude of the growth cycle and in vegetation activity during the middle of the growing season (Myneni *et al.*, 1997; Tucker *et al.*, 2001; Zhou *et al.*, 2001; Fang *et al.*, 2003; Slayback *et al.*, 2003). In our study, bird species that inhabit dense wooded habitats show striking patterns of population increase throughout time (e.g. *Certhia brachydactyla*, *Erithacus rubecula*, *Fringilla coelebs*, *Garrulus glandarius*, *Sylvia atricapilla*, *Troglodytes troglodytes*), and this is also the case with those bird species mainly distributed across central and northern Europe that reach their southern boundary limits in the north of the Iberian Peninsula (see, for example, *Sylvia communis* and *Turdus philomelos* in the Appendix). These short- to medium-term population increases may be due to concomitant increases in productivity (Julliard *et al.*, 2004b). Although the monitoring of birds has mostly been carried out in places that apparently did not suffer great habitat changes during the study period, subtle changes in land use and land cover near the sampling points (e.g. field abandonment and the subsequent increase in forest development) or ecological succession (particularly in areas with little structural complexity) may affect the numbers of birds detected. Nevertheless, we think the marked population increases in woodland birds cannot be explained by intensive land transformations, because forest bird species favour mature habitats that are likely to have changed little during the short study period (only 9 years).

To summarize, we have shown that half of the passerine bird species have exhibited positive population trends in the Iberian Peninsula during the last 9 years, which is good news from a conservation perspective. There are, however, large interspecific differences, which are explained by habitat preferences and climatic characteristics of the geographical ranges of the studied species. Such patterns suggest that net primary production may be brought to discussions on global change as a relevant component to explain recent changes in biodiversity.

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BIOSKETCHES

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Appendix Parameters describing yearly changes in bird counts (population trends from 1996 to 2004) and species autoecological and distributional variables of 57 passerine species in Spain.

		Population growth rate			Dmax	SC	HB	No. UTM	MM	TM
		Slope	SE							
<i>Aegithalos caudatus</i>	R	0.01	0.015	n.s.	17.7	3.7	0.45	3680	187.5	19.0
<i>Alauda arvensis</i>	R	-0.02	0.009	*	10.3	1.3	0.54	2919	189.7	18.7
<i>Anthus campestris</i>	M	0.02	0.02	n.s.	2.4	1.5	0.56	1987	174.6	18.9
<i>Calandrella brachydactyla</i>	M	-0.03	0.017	n.s.	46.9	1.1	0.29	2087	154.3	19.3
<i>Carduelis cannabina</i>	R	0.01	0.007	n.s.	7.7	2.0	0.69	4850	176.4	19.2
<i>Carduelis carduelis</i> †	R	0.04	0.007	***	7.8	3.0	0.80	5093	170.6	19.3
<i>Carduelis chloris</i> †	R	0.08	0.007	***	10.4	2.9	0.50	4795	172.7	19.4
<i>Certhia brachydactyla</i>	R	0.03	0.011	**	12.4	4.4	0.43	3987	183.3	19.1
<i>Cettia cetti</i>	R	0.03	0.008	***	5.6	3.0	0.57	3369	170.4	19.3
<i>Cisticola juncidis</i>	R	0.03	0.012	**	5.7	1.6	0.48	2478	160.8	20.0
<i>Corvus corone</i> †	R	0.02	0.007	**	2.1	3.3	0.72	3249	194.3	18.6
<i>Corvus monedula</i> †	R	-0.03	0.012	**	2.1	2.2	0.55	2563	162.2	19.1
<i>Delichon urbica</i> †	M	0.05	0.011	***	13.5	1.7	0.33	4674	174.7	19.3
<i>Emberiza cirrus</i>	R	0.01	0.011	n.s.	5.8	3.0	0.62	3492	183.3	19.1
<i>Erithacus rubecula</i> †	R	0.06	0.008	***	22.2	4.0	0.62	3093	199.2	18.8
<i>Fringilla coelebs</i> †	R	0.06	0.006	***	23.2	3.9	0.63	4529	180.7	19.1
<i>Galerida cristata</i>	R	-0.01	0.006	*	4.7	2.0	0.55	3973	156.6	19.5
<i>Garrulus glandarius</i> †	R	0.04	0.012	***	8.6	3.7	0.57	3415	191.2	19.0
<i>Hippolais polyglotta</i>	M	0.02	0.013	n.s.	4.9	3.1	0.65	3820	177.3	19.3
<i>Hirundo rustica</i> †	M	-0.03	0.007	***	22.5	1.4	0.40	5200	173.0	19.3
<i>Lanius meridionalis</i>	R	0	0.014	n.s.	0.7	2.5	0.80	3397	161.4	19.4
<i>Lanius senator</i>	M	-0.03	0.011	**	7.4	3.1	0.41	3651	155.5	19.4
<i>Lullula arborea</i>	R	0.01	0.01	n.s.	6.8	2.8	0.90	3482	176.4	19.1
<i>Luscinia megarhynchos</i> †	M	0.04	0.006	***	8.1	3.2	0.90	4117	166.3	19.3
<i>Melanocorypha calandra</i>	R	-0.02	0.008	*	22.2	1.1	0.21	2035	154.3	19.3
<i>Miliaria calandra</i> †	R	0	0.006	n.s.	14.3	2.5	0.55	4508	165.2	19.3
<i>Motacilla alba</i> †	R	0	0.009	n.s.	4.2	2.2	0.39	3999	183.9	19.1
<i>Motacilla cinerea</i>	R	-0.02	0.023	n.s.	3.0	3.1	0.23	2535	198.8	18.9
<i>Motacilla flava</i>	M	0.03	0.015	n.s.	7.7	1.8	0.55	1456	172.5	19.5
<i>Muscicapa striata</i>	M	0.06	0.023	**	1.6	4.0	0.60	2032	169.2	19.4
<i>Oenanthe hispanica</i>	M	-0.02	0.014	n.s.	2.4	2.4	0.71	2962	157.7	19.3
<i>Oenanthe oenanthe</i>	M	-0.02	0.011	n.s.	8.3	1.4	0.66	2380	183.6	18.4
<i>Oriolus oriolus</i>	M	0.08	0.009	***	3.1	3.7	0.60	3897	171.4	19.2
<i>Parus ater</i>	R	0.02	0.012	n.s.	18.8	4.3	0.53	2567	203.9	18.7
<i>Parus caeruleus</i>	R	0.04	0.009	***	25.5	4.0	0.54	4335	181.4	19.1
<i>Parus cristatus</i>	R	0.04	0.016	*	12.7	4.1	0.49	2515	193.9	19.0
<i>Parus major</i> †	R	0.02	0.009	**	10.7	3.9	0.63	5013	175.7	19.3
<i>Passer domesticus</i> †	R	0	0.006	n.s.	60.3	1.6	0.59	5228	172.9	19.3
<i>Passer montanus</i>	R	0.02	0.012	n.s.	8.0	2.1	0.53	2948	173.2	19.2
<i>Petronia petronia</i>	R	0.01	0.012	n.s.	1.7	2.5	0.70	3004	166.7	18.9
<i>Phoenicurus ochruros</i>	R	0.06	0.011	***	4.6	1.7	0.65	3382	193.7	18.7
<i>Phylloscopus bonelli</i>	M	0.06	0.011	***	15.8	4.0	0.62	2508	184.3	18.7
<i>Phylloscopus coll-iber</i>	R	0.02	0.018	n.s.	13.4	4.0	0.57	2184	211.1	18.9
<i>Pica pica</i> †	R	0.02	0.006	**	5.7	2.9	0.71	4290	178.8	19.1
<i>Regulus ignicapillus</i>	R	0.04	0.015	**	18.1	4.2	0.55	2357	203.5	18.9
<i>Saxicola torquata</i>	R	0.01	0.009	n.s.	6.5	2.1	0.70	4628	177.4	19.3
<i>Serinus serinus</i> †	R	0.03	0.005	***	13.3	3.2	0.77	5154	174.6	19.3
<i>Sturnus unicolor</i> †	R	0.03	0.007	***	11.6	2.8	0.60	4806	170.3	19.3
<i>Sylvia atricapilla</i>	R	0.05	0.009	***	12.2	4.0	0.62	3465	189.3	19.0
<i>Sylvia cantillans</i>	M	0.03	0.014	*	13.6	3.3	0.77	2642	169.1	19.0
<i>Sylvia communis</i>	M	0.06	0.014	***	8.4	3.0	0.70	1761	197.1	18.7
<i>Sylvia melanocephala</i>	R	0.03	0.008	***	15.3	3.1	0.82	3073	157.3	19.8
<i>Sylvia undata</i>	R	-0.02	0.014	n.s.	17.7	2.4	0.45	3582	180.3	19.2

Appendix *Continued*

		Population growth rate			Dmax	SC	HB	No. UTM	MM	TM
		Slope	SE							
<i>Troglodytes troglodytes</i>	R	0.05	0.008	***	33.5	3.7	0.73	3730	188.9	19.0
<i>Turdus merula</i> †	R	0.05	0.008	***	19.6	3.6	0.74	5143	175.4	19.3
<i>Turdus philomelos</i>	R	0.09	0.015	***	4.2	4.7	0.32	1666	218.6	18.8
<i>Turdus viscivorus</i>	R	-0.01	0.016	n.s.	7.2	4.0	0.56	3369	184.7	19.0

The instantaneous growth rate (obtained from the linear trend with time assuming Poisson's error distribution and using a log-link function) is presented as the slope, its standard error (SE) and the significance of the deviation from 0 (null hypothesis of no yearly population change; n.s., non-significant, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Migratory status: R, resident; M, trans-Saharan migrant. Relative abundances (a proxy for maximum ecological density, Dmax in birds/10 ha). Structural complexity index (SC; a small number denotes poorly vegetated habitats, while large values refer to habitats with high structural complexity and vegetation volume; 0, lacking or very sparse vegetation cover; 1, pasturelands; 2, shrublands with sparse vegetation cover made up of bushes lower than 0.5 m; 3, thick shrublands with bushes higher than 0.3 m in height; 4, parklands, narrow riparian woods, hedgerows, young forests; 5, dense mature forests with trees usually higher than 12 m). Habitat breadth (HB): number of UTM squares (10 × 10 km) occupied in Spain (no. UTM); average spring rainfall (mm; MM) and temperature in June (°C; TM) of the areas occupied by each species in the Iberian peninsula.

†Common species easily recognizable.